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ALYTES

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Declining amphibian populations – a global phenomenon ?* Findings and recommendations**

Amphibian populations are in decline in many parts of the world – in some cases and in some areas to the point of extinction. Much of the decline is attributable to obvious habitat destruction or modification. However, the decline of populations even in protected areas indicates that more subtle effects are involved. Where data are available, anthropogenic factors, such as acid precipitation, pesticide release, agricultural practices, land-use changes, and introductions of exotic species have been important in bringing about these population changes. Although other organisms certainly are affected by the same factors, amphibians are particularly sensitive bioindicators because of their permeable skins, biphasic life history, pattern of embryonic development, aspects of their population biology, and the complexity of their interactions in communities and ecosystems. Several study programs should be initiated, including carefully planned and integrated long-term studies of populations and key communities, analyses of bibliographic and museum data, and resurveys of previously studied populations. In the immediate future, the findings of the workshop should be disseminated widely and the desirability of a conference to deal with issues such as the use of amphibians in biomonitoring, analyses of factors involved in declines, and future directions in integrated approaches to the world-wide crisis in loss of biodiversity should be explored. Careful evaluation should be given to proposals for new public (such as a National Institute for the Environment) or private organizations that would give attention to taxon-centered as well as more global monitoring and study programs in the area of biodiversity.

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* This is the title of a workshop, sponsored by the Board on Biology of the National Research Council of the U.S.A., which was held at the Arnold and Mabel Beckman Center (Irvine, California, U.S.A.) on 19-20 February 1990.

** The conclusions, opinions, and recommendations contained in this article are those of the workshop participants and do not necessarily reflect the views of the National Research Council or the National Academy of Sciences of the U.S.A.

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Source : MNHN, Paris

INTRODUCTION

The workshop was organized because of an increasing awareness among biologists around the world that many populations and species of amphibians (frogs, order Anura; salamanders, order Caudata; caecilians, order Gymnophiona) have experienced declines and extinctions, even in protected natural areas. Internal funding from the National Research Council was obtained in November 1989 by the Board on Biology, and a workshop was organized by David B. WAKE and Harold MOROWITZ, members of the Board on Biology, and by the staff of the Board. The workshop included presenters of information and discussants representing an array of disciplines (see Appendix).

FINDINGS

The workshop addressed the proposition that " worldwide, amphibian populations are in decline. " To a degree, this is true, but the statement is not universally applicable to all taxa in all locations, nor is there evidence of a single planetary causal factor. Drastic habitat modification by humans is a major cause of decline in amphibian populations, but other human activities are also important. However, the decline and extinction of some amphibian populations in seemingly pristine areas cannot be directly tied to human activities.

I. DATA-BASED CONCLUSIONS

A. Many montane species of western North America are in decline, even in protected preserves and undisturbed areas where habitat alteration is not apparent. Montane areas in other regions of the New World also have declining amphibian populations (e.g., Middle America, Atlantic Coastal forest of Brazil). Frogs from some low elevation sites in different parts of the world are declining or have disappeared. Many declines first became evident in the period between 1978 and 1982, although some occurred earlier.

B. Populations of several species in different areas (northwestern United States, southern and eastern Canada, and eastern Australia) have experienced severe declines at many sites, but data are fragmentary.

C. Populations in some regions, such as the southeastern United States, show little evidence of general declines, apart from that clearly attributable to habitat destruction.

D. In some habitats, declining and stable species co-occur; for example, populations of the Wood Frog, *Rana sylvatica*, appear to be stable in the Rocky Mountains, but populations of the Leopard Frog, *Rana pipiens*, in the same area are declining. Accordingly, there is species-specificity in the response to factors causing declines.

(1) Reasons for species specificity may be attributable in part to differences in physiological (e.g., tolerance to low pH), behavioral, ecological (e.g., short developmental period), or other properties.

Source : MNHN, Paris

(2) Declining and stable species sometimes are related phylogenetically, such as being members of the same genus.

(3) Certain species are experiencing difficulty over broad regions, yet appear to be doing well in other locations.

E. No evidence was presented for declines of populations living at low elevations in equatorial regions (between 10 degrees N and S latitude), except in areas of severe habitat destruction (e.g., timber harvest, agricultural practices such as grazing and irrigation, desertification). Information from long-term studies is available only for Borneo and Panama.

F. Where declines and extinctions are documented, we generally do not know which stages of the life cycle are most affected. No specific pathologic conditions thus far have been identified to suggest a unifying theme for the declines; however, infectious disease agents or toxins have not been adequately studied and cannot be ruled out as possible causative factors.

G. About 5,000 species of amphibians have been described throughout the world, with most species being found in the tropics. In general, little is known about the status of most species. However, evidence is available from a wide variety of sources to support the main finding of decline in many species and in many areas.

II. ANTHROPOGENIC FACTORS

A. Anthropogenic factors have been and continue to be important in population declines and local extinctions in most areas. These include acid precipitation, heavy metal discharge and mobilization, pesticide release, deforestation, hydrological modification and changes in patterns of land-use (urbanization, changed agricultural practices, extention of agriculture to wetlands, release of irrigation waters, and the like).

B. Wildlife management practices, such as the stocking of previously pristine lakes and streams with fish that are predators of amphibians, have contributed substantially to declines in some areas.

C. In two cases (western North America and eastern Australia), the introduction and subsequent proliferation of non-native anurans (the Bullfrog, *Rana catesbeiana*, for food and sport, and the Cane Toad, *Bufo marinus*, as a biological control of insect pest) have contributed to the decline of native amphibians. Populations of the Bullfrog (even introduced populations) are now in decline in many areas, but the Cane Toad is thriving and has become a pest itself in Australia.

III. SPECIAL PROPERTIES OF AMPHIBIANS

A. Amphibians are sensitive *bioindicators* of environmental change because of their physiological and behavioral characteristics, life-historical and morphogenetic patterns, and features of their population biology.

Source : MNHN, Paris

B. The skin of amphibians is highly permeable to gases and liquids in the environment; as a result amphibians are intimately exposed to materials in the water, air, and terrestrial substrate.

C. High fecundity, complex life cycles (with larval and adult stages usually occupying different habitats), and fragmented but interconnected population structures may render amphibians sensitive to diverse environmental factors relative to other vertebrates. Biotic and abiotic factors impinge on amphibians in many ways. Development in many frogs takes place in water, and tadpole consume mostly plant materials. Special conditions must be met in order for metamorphosis to succeed. Metamorphosed animals typically are terrestrial or semi-terrestrial, and invertebrates (especially insects) are major prey. Accordingly, those factors that affect riparian and aquatic vegetation and insects can also affect larval and adult amphibians. In some regions, adults may also undergo seasonal aestivation and hibernation, and they are thus subject to additional environmental factors. Populations often occur as subpopulations in neighboring ponds, and individuals may breed in one pond during one year, but another the next. These features combine to expose amphibians to a wide variety of influences during their lives.

While the life history outlined above is well known and is typical of many species, amphibians are a very diverse group. Most caecilians, about one-half of the species of salamanders, and hundreds of species of frogs are strictly terrestrial throughout their lives, and other species of all three groups are strictly aquatic. Some salamanders are permanent larvae, and many species in all groups have direct development with no larval stage. A few frogs and salamanders are live-bearing, and most caecilians are viviparous. This diversity in development, life history and ecology adds to the suitability of the group as a whole for studies of biodiversity.

D. The additive or synergistic effects among a number of global, regional and local factors may result in substantial declines.

E. Environmental acidity appears to play a major role in declines of amphibian populations. Some species have evolved in low pH environments, but many others have not experienced acidity in their evolutionary history and so are especially sensitive to lowering of pH, and the toxicity of metals such as aluminum that are biologically active at low pH, during specific phases of embryogenesis.

Recommendations

The stresses on most declining amphibians and their habitats are of human origin. Anthropogenic effects on the scale of global to local environment are complex, and their remediations will require an understanding of ecosystem functions. The pursuit of such studies depends on the knowledge, skills and cooperation of scientists from many disciplines. Such research will inevitably be labor-intensive and will require use of modern technology. This will demand a broad range of new human and financial resources.

Recommendations are grouped in four general categories.

Source : MNHN, Paris

I. LONG-TERM STUDIES OF AMPHIBIAN POPULATIONS ARE NEEDED, WITH SPECIAL EMPHASIS ON THE FOLLOWING

A. *Studies focusing on the significance of amphibians in ecosystems*

The significance of salamanders in ecosystems needs clarification. In some ecosystems (e.g., at Hubbard Brook, N.H.), amphibians have been shown to have the greatest animal biomass, but little information is available for other areas. New studies should focus on the role of both larval and adult amphibians in the food web, and the unique potential of amphibians as indicators of the health of the ecosystem. Such studies should be established at selected strategic sites around the world, or incorporated into ongoing programs. Ideally, these studies will be conducted within the context of long-term population studies.

Amphibians have properties which make them especially useful *bioindicators* in ecosystem studies. Specific reasons are listed below.

(1) Most species have complex life cycles, with both aquatic and terrestrial phases.

(2) Amphibians have permeable skins, which result in large and rapid material exchange with the environment including water, air, and terrestrial substrate. Because of their susceptibility to different factors, they are especially sensitive early-warning indicators of certain types of environmental changes.

(3) Amphibians are small to intermediate-sized vertebrates; their fate has direct relevance to that of other vertebrates, including humans. They are high in the food web, and their decline is a signal of deeper ecosystem deterioration, including factors reducing populations of invertebrates and plants.

(4) Amphibian biomass constitutes an appreciable fraction of many terrestrial ecosystems; they have been shown to be the dominant vertebrate group in some ecosystems.

(5) The demise of amphibians has inevitable, major effects on other components of ecosystems.

B. *Studies focusing on the population biology of amphibians*

We recommend that long-term population studies be conducted to identify abiotic and biotic factors that account for temporal patterns of diversity and abundance of amphibians under unaltered conditions, so that baseline data can be generated and amphibians can serve as indicators of environmental change in ecosystems. Depending on local diversity, these studies will deal with entire assemblages or with focal species. Such studies should be distributed geographically to take into account patterns of diversity based on differences in latitude, elevation, habitat, and taxonomy. Of special importance is the interaction between habitat fragmentation and population structure. Long-term monitoring in these studies should focus on:

(1) Population dynamics, including age-specific birth and death rates, mechanisms of population regulation, and demographic responses to pollutants.

Of special importance is an understanding of the spatial and temporal patterns of

Source : MNHN, Paris

fluctuation in population size through time, which relates directly to long-term persistence and vulnerability of isolated populations and populations inside nature preserves that are surrounded by degraded habitats.

(2) The relationship of physical and chemical variables in the environnement to the changes in the amphibian populations being studied.

Care must be taken to standardize the collection and analysis of physical variables and to design population studies to allow for the unique characteristics of each system. Experiments should be designed to test hypotheses generated by long-term monitoring studies. Success of this phase requires formal and regular communication among research groups as well as dependable long-term support. Attempts should be made to integrate population and ecosystem studies, where feasible. Renewable funding intervals should extend over periods of five years or longer, because life spans of amphibians are relatively long and the dynamics of population cycles (related to variable weather and other factors) must be understood over a relatively long time frame to allow valid interpretations of the data.

C. *Studies focusing on the relationship of chemical and physical factors to individual organisms and populations*

Efforts must be made to identify possible chemical and physical causes of amphibian decline on a broad scale. Because different causes probably account for the decline of different populations, we propose the careful selection of specific populations with documented declines for special study. The target of such studies should be species with complex life cycles. Embryonic and larval development should be compared in water where the eggs were found, and in water of known high quality. The water samples should be analyzed for their chemical constituents, including major ion concentrations, pesticides, herbicides, and other components of the environment. Selected individuals should be followed from early development through sexual maturity, in order to detect possible stage-specific effects. Meteorological conditions such as temperature, humidity, rainfall, ultraviolet intensity and atmospheric ozone at the collection sites should be monitored continuously.

Moribund and dead specimens should be collected for pathological studies, to include histologic, microbiologic, and toxicologic analyses. Healthy control animals should be submitted for study at the same time.

II. Compilation of information, and use of historical data

Many past studies contain critical information about amphibians, including historical occurrence, population density, survivorship of various life history stages, and other variables. We recommend that as far as possible future studies be designed to take advantage of these prior investigations, which can serve as baselines. Such information will

Source : MNHN, Paris

be especially valuable in regions where amphibian populations are known or suspected to be in decline.

A. *Much useful information can be derived from museum records and the literature*

There is a rich data base in the collections of the natural history museums of the world, and in publications. There are also some other sources of information, such as records of field stations and long-term but unpublished studies by individual investigators. These sources should be utilized thoroughly. We recommend that full advantage be taken of bibliographic and museum data, so that we might be better able to detect changes in amphibian populations that occur over long time intervals (decades or even centuries). This method would take advantage of the large, existing data sources and would be particularly useful in detecting both changes in distribution and relative abundance, given an understanding of the limitations and advantages of such data. Most important, identified changes then could be correlated with a variety of morphological, ecological, climatic, geographic and phylogenetic parameters that can assist in identifying problem groups, areas, or conditions, and relevant factors responsible for such declines and extinctions.

B. *Ecological and population data from previous studies should be evaluated to determine if they can be used as a base for comparative studies*

This is an approach that will develop a series of samples from two or more periods of time. If such studies are amplified sufficiently they will produce enormous quantities of information at relatively low cost. The following sampling approaches should be undertaken:

(1) Resurvey of previously studied populations.

In many instances it may be possible to resurvey the exact sites at which prior studies were conducted, and it may be possible to convince the original investigators to return to these sites so as to control as much as possible for methods of sampling.

(2) Surveys of historical localities derived from museum and literature records, and from unpublished field notes of investigators.

Areas to be studied would be selected to represent diverse taxa and geography, and would include areas showing population declines. Protocols for sampling must be developed for each taxon and region in order to assess accurately the presence or absence of a population, and in certain cases, aspects of population structure. This is especially important because many amphibians are secretive organisms, difficult to find except when they are breeding.

Source : MNHN, Paris

III. INVESTIGATE THE FEASIBILITY AND DESIRABILITY OF ESTABLISHMENT OF A NEW ORGANIZATION, WHICH WOULD BE FOCUSED ON ISSUES OF MAINTENANCE OF BIODIVERSITY

Existing environmental organizations and governmental organizations often fail to respond appropriately and promptly to the kinds of crises and challenges described here. Institutional structural changes or innovations may be needed. We recommend that the Board on Biology examine this problem, and initiate one or more formal studies with the following parts:

A. An analysis of the benefits and disadvantages of different institutional models, both governmental and non-governmental, for the support and funding of research of the following general kinds:

(1) The discovery, testing, and utilization of taxa and interacting subsets of communities and ecosystems that will permit and facilitate early detection of environmental deterioration.

(2) The development of guidelines aimed at the management of natural systems and for remedial actions in such systems.

B. An analysis of organizational mechanisms that would maximize the flexibility and efficiency of institutions; among these might be peer review processes, rotation of advisory board membership, and establishment of program priorities and directions.

A proposal has been made by another group of concerned individuals for the establishment of a National Institute for the Environment (N.I.E.). It is possible that one role of such an organization would be the function we have outlined. Accordingly, an alternative recommendation is that the Board on Biology conduct a study based on the proposal for N.I.E.

IV. DESIGN AND DEVELOPMENT OF EDUCATIONAL PROGRAMS THAT WOULD KEEP THE PUBLIC INFORMED CONCERNING THE STATUS OF POPULATIONS AND SPECIES OF CRITICAL TAXA (SUCH AS AMPHIBIANS) AROUND THE WORLD, AND OF THEIR SIGNIFICANCE FOR ISSUES IN BIODIVERSITY

V. IN ADDITION TO THE MAIN LONG-TERM RECOMMENDATIONS, SEVERAL IMMEDIATE ACTIONS SHOULD BE TAKEN

A. Distribute a summary of the main results of this workshop in appropriate outlets.

B. Distribute the main findings and recommendations of this workshop to appropriate organizations and individuals, including workshop participant.

C. Convene a more specialized workshop, symposium or meeting with the tentative title: *Declining amphibian populations: biomonitoring, analyses of factors and future*

Source : MNHN, Paris

directions. Such a meeting would: (1) compile and analyze the current data on declining populations, using present trends to predict future changes in species richness and diversity; (2) identify critical areas in need of intensive study; (3) develop a protocol for long-term monitoring of selected amphibian populations, species and communities, with consideration of the relationship of amphibians to the dynamics of ecosystems, the patterns of amphibian population dynamics, and the identification of critical physical and chemical parameters for amphibian life history; and (4) study and recommend sources of funding for long-term investigations. The workshop should include both amphibian biologists and experts in the subject areas relevant to the problems considered (e g., ecotoxicology, climatology, water quality, physiology, development, population biology, wildlife and fisheries, systematics).

D. Establish a committee to organize a large-scale international symposium and seek funding for it [perhaps under the aegis of the International Society for the Study and Conservation of Amphibians (ISSCA)].

E Improve communication among members of the biological community concerned with amphibian diversity, population biology and ecology. The International Society for the Study and Conservation of Amphibians is an existing organization that might well serve this function.

APPENDIX

WORKSHOP PARTICIPANTS

Chairman: David B. WAKE, University of California, Berkeley.
Co-Chairman Harold J. MOROWITZ, George Mason University, Virginia.

SPEAKERS

Andrew BLAUSTEIN, Oregon State University, Corvallis.
David BRADFORD, University of California, Los Angeles.
R. Bruce BURY, National Ecology Research Laboratory, U.S. Fish and Widlife Service, Ft. Collins, Colorado
Janalee CALDWELL, University of California, Los Angeles.
P Steven CORN, National Ecology Research Laboratory, U.S. Fish and Wildlife Service, Ft. Collins, Colorado.
Alain DUBOIS, National Museum of Natural History, Paris.
John HARTE, University of California, Berkeley.
Marc HAYES, University of Miami, Florida.
Robert INGER, Field Museum of Natural History, Chicago.
H.-K. NETTMANN, University of Bremen, Federal Republic of Germany.
A. Stanley RAND, Smithsonian Tropical Research Institute, Panama
David SMITH, Williams College, Massachusetts

Source : MNHN, Paris

Michael TYLER, University of Adelaide, Australia.
Laurie VITT, University of California, Los Angeles (and Savannah River Ecology Laboratory, South Carolina).

COMMENTATORS AND ANALYSTS

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Bassett MAGUIRE, University of Texas, Austin.
Richard MONTALI, National Zoological Park, Washington, D. C.
Vaughan SHOEMAKER, University of California, Riverside.
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Richard TURCO, University of California, Los Angeles.
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Henry WILBUR, Duke University, North Carolina.

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Source : MNHN, Paris

Declining amphibian populations – a global phenomenon? An Australian perspective *

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Evidence that populations of at least 10 % of the Australian amphibian species are subject to serious decline is reviewed. Causal factors can currently be identified in just a few of these cases. On the other hand, a few amphibian species are expanding their range in Australia, but this phenomenon is much more limited in scope.

INTRODUCTION

Anurans are the only amphibians native to Australia. A few species of caudates have been imported by aquarists; one of them (the axolotl) has been released in the wild in Tasmania and has become established there.

A significant proportion of the Australian frog fauna has been discovered or described within the past 30 years. MOORE (1961) recognised 90 species throughout the continent. My current estimate is that there are 194. I am aware of descriptions of five new species in press and I estimate that at least 25 more species remain to be discovered or described

Because Australia is a vast continent with a small population and few herpetologists, it is understandable that increases or decreases in the frequency of occurrence of frog species often need to be dramatic to attract comment. Comments by OSBORNE (1986, 1989) are noteworthy.

In fact concerned Australians have been exposed to evidence of an environmental disaster created by the *expansion* of an amphibian population: the colonisation of the continent by the introduced species *Bufo marinus*. The fact that the Prime Minister, Mr.

* This paper was presented during the workshop on " Declining amphibian populations a global phenomenon? ", organised by the Board on Biology of the National Research Council of the U S A , which was held at Irvine (California, U.S.A.) on 19-20 February 1990

Source : MNHN, Paris

Bob HAWKE, made a commitment to fund research to control this species in a 1989 statement on his government's environmental policy, is a clear indication of the serious concern about the only amphibian species in the world to be declared a pest.

Against a background of the proliferation of an amphibian species, it follows that evidence of decline of native species needs to be dramatic to be heeded. Unfortunately, there is now ample evidence of serious localised declines affecting at least 10 % of the Australian frog fauna.

These declines have occurred within the last decade and there are two examples of possible extinction of species: the gastric brooding frog *Rheobatrachus silus* and *Taudactylus diurnus*.

NORMAL POPULATION FLUCTUATIONS

Under certain geographic and climatic conditions, enormous fluctuations occur in the populations of a number of species of Australian frogs. This is particularly evident in the arid northeastern deserts of South Australia, where maximum temperatures average 36-39°C in summer (ALLAN, 1990). Median annual rainfall is 100-150 mm, whilst mean annual evaporation exceeds 3600 mm (KOTWICKI, 1986, 1987). Periodic flooding of the area principally from creeks flowing down from the Northern Territory and from Queensland, transport frogs which breed and proliferate to form massive populations in temporary, freshwater lakes. Subsequent periods of aridity produce total extinction of those populations Thus the frog fauna of that area exhibits great cyclic swings from millions to zero. These events are normal, anticipated and acceptable to a human observer.

It is possible that wild fluctuations also occur in temperate forest. The evidence is partly circumstantial but compelling. As discussed by CZECHURA (1990), the evidence partly hinges upon the question of why newly discovered species are found in abundance in areas previously sampled Classic examples are *Rheobatrachus silus* and *Taudactylus diurnus* in southeast Queensland, and *Litoria brevipalmata* in northern New South Wales (G. F. WATSON, in litt.). Each instance was followed by a dramatic decline that can be dated (see p. 45)

DATA SOURCES

Very few declines of frog populations have been documented in the literature. In assembling data at the instigation of Dr. D. B WAKE, I wrote to colleagues throughout Australia. For their responses I am indebted to the following:

K. R. MCDONALD, Queensland National Parks & Wildlife Service, Townsville.
- G. F. WATSON, Department of Zoology, University of Melbourne, Melbourne.
- M. J. LITTLEJOHN, Department of Zoology, University of Melbourne, Melbourne.
- L. A. SMITH, Western Australian Museum, Perth.

Source : MNHN, Paris

- J. D. ROBERTS, University of Western Australia, Perth.
- J. WOMBEY, C.S.I.R.O. Division of Wildlife & Ecology, Canberra.
- G. V. CZECHURA, Queensland Museum, Brisbane.
- M. KING, Northern Territory Museum & Art Gallery, Darwin.
- W. OSBORNE, Canberra College of Advanced Education, Canberra.
- R. G. BECK, Lynwood Park, Mil-Lel, South Australia.
- G. C. GRIGG, Department of Zoology, University of Queensland, Brisbane.

GEOGRAPHIC DISTRIBUTION OF DECLINING POPULATIONS

All of the reports of species in decline are within the southern half of the continent, and the majority of these border the Great Dividing Range in the east and southeast (fig. 1).

SPECIES SUBJECTED TO DECLINE

Although I do not dispute statements that frogs are not as plentiful as they used to be in certain areas, I have included in Table I only those where there is evidence of a substantial change in abundance or significant contraction of range

I have excluded contractions of range readily attributable to local urbanisation and land clearance. I have focussed attention upon those species in which there has been a dramatic decline over the past decade. This time frame is significant, for insofar as I can gather the crucial changes probably commenced in the period 1979-1983.

LIKELY CAUSAL FACTORS

It is possible to identify the causal events of declines of just a few species included in Table I.

For example, the apparent disappearance of species at Lake Dumbleyung in Western Australia has been attributed to salination The problem is widespread in parts of Australia, but the variation in capacity to withstand high salt levels appears to be associated with skin thickness. However, it is presumably the aquatic embryos that are vulnerable.

The dependence of frogs upon moisture, and the severity of droughts in Australia permits the obvious conclusion that drought must be a potential significant factor producing localised extinctions. The drought in 1982-1983 in southeastern Australia that was a consequence of the El Niño must have produced localised extinctions, but not on the scale that has been observed.

The demise of *Rheobatrachus silus* occurred in about 1980 The significance of the species because of its unique habit of gastric brooding meant that it was the subject of

Source : MNHN, Paris

Fig. 1 - The geographic zones where declines of frog populations have been noted in Australia (hatched).

Source : MNHN, Paris

Table I. – Species of Australian frogs exhibiting declines.

Species	Geographic area affected	Significance of decline
Crinia georgiana	Lake Dumbleyung, W A.	unknown
Geocrinia laevis	S. & Central Victoria	unknown
G. victoriana	S. & Central Victoria	unknown
Heleioporus eyrei	Perth metropolitan area	unknown
Limnodynastes dumerilii	S.E. South Australia, S. & Central Victoria	unknown
L. tasmaniensis	S.E South Australia, S. & Central Victoria	unknown
Litoria adelaidensis	Lake Dumbleyung, W.A.	unknown
L. aurea	Uncertain At least from southern N.S.W.	serious
L. ewingi	S. & Central Victoria	unknown
L. flavipunctata	A.C.T. & N.S.W.	serious
L. lesueuri	S E. Qld.	unknown
L. pearsoniana	S.E. Qld.	serious
L. raniformis	S.E. S.A., S. & Central Victoria	unknown
L. spencerii	Victoria	unknown
L. verreauxii	A.C.T.	unknown
Pseudophryne bibroni	S.& Central Victoria, southern N.S.W.	unknown
P. corroboree	A.C.T. & S. N.S.W.	unknown
P. dendyi	S. & Central Victoria	unknown
P. semimarmorata	S.E. South Australia, S. & Central Victoria	unknown
Rheobatrachus silus	S.E. Qld.	serious - possibly extinct
R vitellinus	Central eastern Qld.	serious
Taudactylus diurnus	S.E. Qld.	serious - possibly extinct
T. eungellensis	Central eastern Qld.	serious

Source : MNHN, Paris

extensive investigation and had a high public focus. Consequently its disappearance was examined very closely which, for the purposes of this conference, was fortuitous In fact its disappearance typifies the problem that we address.

Rheobatrachus silus was discovered and described in 1973. It was abundant in rainforest within a two hour drive of Brisbane. It was so abundant that an agile collector could have picked up 100 in a single night. In 1974, CORBEN et al. reported the habit of gastric brooding, but several years elapsed before a photographic record of birth was obtained (TYLER & CARTER, 1981) And it was in 1981 that the species totally disappeared in the wild. A captive colony was maintained in Adelaide for two further years.

The original distribution of the species was confined to the Conondale and Blackall Ranges and occupied less than 100 km. The only population estimate was made by INGRAM (1983), who arrived at a figure of 77 within his study site of 0.7 hectare.

The disappearance occurred over winter. The failure to locate individuals during winter was a normal phenomenon. Thus it was several months before the absence was recognised for what it was.

TYLER & DAVIES (1985) reviewed the following hypotheses that has been put up to explain the demise:

(1) over-collecting by herpetologists;
(2) pollution of creeks brought about by logging;
(3) pollution of creeks caused by damming of sections associated with gold-panning;
(4) drought.

Each of these suggestions proved incapable of explaining the disappearance of the species. It is worth observing that the species disappeared simultaneously from the Kondalilla National Park.

This phenomenon of apparently inexplicable decline or disappearance is repeated time and again in eastern Australia. *Taudactylus diurnus* whose range overlapped that of *R. silus* also disappeared without trace. It had been even more abundant.

The demise or serious declines of the 22 species listed has taken place whilst other species have expanded their ranges. It is possible that an appreciation of those success stories may contribute to an understanding of the modern failures.

EXPANDING POPULATIONS

An account of the colonisation of Australia by *Bufo marinus* conforms to the tragic list of introduced exotic species. A total of 102 individuals were imported in 1935 and their offspring released at a series of sugar cane plantations on the Queensland coast. The intention was to provide a biological control of insect pests of sugar cane. That objective was not achieved and the toads had an impact that was not anticipated. Being toxic they brought about the death of native animals that included amphibians in their diet. Having a high fecundity they proliferated to such an extent that they decimated the ground-

Source : MNHN, Paris

dwelling invertebrate fauna and, in the absence of significant predators, extended their range beyond the cane plantations to a degree that was not conceived. The toads now occupy 600,000 km and are moving west into the Northern Territory at at least 20 km per year (TYLER, 1989). Serious attempts are being made to find an effective control agent.

One of the Australian native species may be expanding its range. The small marsh frog *Limnodynastes tasmaniensis* of southeast and east Australia appears adept at establishment following accidental transportation. They were discovered at Kununurra in the northwest of the continent in 1977 (MARTIN & TYLER, 1978) and at Mound Springs in the outback of South Australia in 1976 (TYLER, 1978) It will be noted from Table I that *L. tasmaniensis* numbers in the moister southeast have declined.

It has been suggested that in northern Australia frog numbers may have increased as a direct result of human modification of the environment (TYLER, 1979). Road construction (whether sealed or unsealed) is accomplished by the quarrying of road building materials for foundations. These excavations, " borrow pits ", may be up to 300 × 100 m in extent. They hold water during the wet season. Being ephemeral water sources they do not support aquatic predators of tadpoles such as fish. They constitute ideal breeding sites for frogs and they have surely effected an increase in frog population densities in the areas in which they occur.

In arid regions, excavation of permanent water sources with steep sides, and known as " turkey nest " dams, has provided refuges for species such as *Litoria latopalmata* and *Crinia deserticola*. There are also commensals such as the green tree frog *Litoria caerulea* that inhabit homes, outhouses and particularly toilets in seasonally arid areas.

These " artificial " habitats have no doubt provided a secure environment for a few species of frogs that are capable of exploiting such opportunities. Despite that positive aspect, the decline of populations is of a different order of magnitude. I do not believe that that decline can be attributed directly to human causes, although there may be contributory factors.

RÉSUMÉ

Cet article présente les informations disponibles sur le déclin des Amphibiens en Australie. Ces informations sont incomplètes, mais elles indiquent que des populations d'au moins 10 % des espèces d'Amphibiens du pays manifestent un déclin important. Dans la plupart de ces cas, les causes n'en sont pas encore connues. Par ailleurs, quelques espèces d'Amphibiens voient actuellement leur aire de répartition en Australie augmenter, mais ce phénomène est d'une ampleur bien plus limitée que le précédent.

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A developmental table of *Crinia signifera* Girard, 1853 (Anura, Myobatrachinae)

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Embryonic development of the Australian frog *Crinia signifera* is described and illustrated. Most of the divergences found in a comparison with related frogs of the *Geocrinia laevis* complex appear to be connected with their different life histories. The applicability of the staging table of GOSNER (1960) and of the table modified for *Geocrinia* (GOLLMANN & GOLLMANN, 1991), is evaluated.

INTRODUCTION

Crinia signifera Girard, 1853 is a small, widespread and abundant frog of Southeastern Australia (Myobatrachidae, Myobatrachinae). It shows an opportunistic reproductive strategy, spawning in a wide range of often rather unpredictable habitats throughout an extended breeding period. Oviposition is aquatic, usually in shallow water after rain The eggs are deposited singly or in small groups, often attached to plants (COGGER, 1986; WILLIAMSON & BULL, 1989).

Early embryonic development, up to the onset of heart beat, follows the " typical " anuran pattern; MOORE (1961) used the development of *Rana sylvatica* (POLLISTER & MOORE, 1937) as a reference. Later embryonic development in *Crinia* diverges from this " typical " pattern, most obviously by the complete absence of external gills. Consequently, most staging tables developed for other anurans (e.g. POLLISTER & MOORE, 1937, GOSNER, 1960) cannot be used for *C. signifera* during this phase of development In studies of embryonic development in related frogs of the *Geocrinia laevis* complex, we developed a modified staging table (GOLLMANN & GOLLMANN, 1991), using the table of GOSNER (1960) as a frame of reference and redefining stages when necessary.

It appeared worthwhile to compare the embryonic development of *Crinia* and *Geocrinia*, which differ markedly in their life histories. Frogs of the *G. laevis* complex deposit their eggs on land; hatching occurs at an advanced tadpole stage, after the spawn has been flooded (LITTLEJOHN & MARTIN, 1964). Moreover, a detailed study of the development of *C. signifera* provided a test case to see whether the staging table developed for *Geocrinia* could be applied to related genera.

Source : MNHN, Paris

The assignment of *C. signifera* to genus and family has been subject to debate BLAKE (1973) resurrected the genus *Ranidella* Girard, 1853. The validity of this action was questioned by HEYER et al. (1982). I take the more conservative approach, using the generic name *Crinia*, without wanting to express an opinion on this taxonomic problem. Likewise, the use of the name Myobatrachidae for what were formerly known as the Australian members of the Leptodactylidae is controversial (TYLER, 1989). However, the subfamily Myobatrachinae (containing both *Crinia* and *Geocrinia*), which is recognized in all current classification schemes, seems to be a well defined taxon (see e.g. WATSON & MARTIN, 1973). Relationships within the Myobatrachinae are less clear: before the study of BLAKE (1973), the species contained in *Crinia* and *Geocrinia* were regarded as congeneric; recent immunological investigations (MAXSON & ROBERTS, 1985) suggest that these two genera are not very closely related and may have diverged already in the late Cretaceous.

MATERIAL AND METHODS

Three amplectant pairs of *C. signifera* were collected in a small temporary pool 5 5 km ENE of Yan Yean, Victoria (37°33′ S, 145°10′ E), on the evening of 10 April 1989 They were transported in plastic bags to the University of Melbourne. Each pair was then put into a small aquarium containing approximately 1.5 l of 5 % Holtfreter's solution and a few stems of *Ceratophyllum* sp. The aquaria were placed in a room with natural light and a temperature of about 20°C. By the next morning, all three pairs had spawned. In the afternoon of 11 April, about 20 eggs of each clutch were put into a Petri dish of 10 cm diameter, containing 5 % Holtfreter's solution, and transferred into a constant temperature room set at 15°C, with a 12 hour light-12 hour dark rhythm. They were inspected under a dissecting microscope at intervals of about 24 hours each morning; on the third and fourth day additional controls were made in the afternoon (six and eight hours, respectively, after the first one).

Egg diameters of ten eggs per clutch were measured with an ocular micrometer before the onset of neurulation (stage 12). Photographs of an embryo were taken daily from the third to the fourteenth day. After the animals had completed embryonic development, they were released in the pond where their parents had been collected and released after having spawned in the laboratory

RESULTS

At late stage 12 (GOSNER, 1960), eggs were about 1.3 mm in diameter. Cleavage, blastular and gastrular stages as well as the closing of the neural folds of the embryos of *C. signifera* conform to the typical pattern of anuran development. The tail bud (GOSNER stage 17) grows out dorsally (MOORE, 1961) Despite the resulting unusual U-shape of the embryo (fig. 1A), GOSNER's table can be used to identify developmental stages up to stage 19 (onset of heart beat; fig 1B, C). For stages 20 to 26, I used the staging table developed for *Geocrinia* by GOLLMANN & GOLLMANN (1991). These stages are defined as follows:

Source : MNHN, Paris

stage 20: mouth open; stage 21: first appearance of expanded melanophores; stage 22: choroid fissure closed; stage 23: eye entirely black, stage 24: 1-2 rows of labial teeth; stage 25: 3-4 rows of labial teeth; stage 26: 5 rows of labial teeth.

Crinia signifera can be staged according to this table, since the characteristics used to define the stages can be observed in the same order as they appear in *Geocrinia*. In the following description of the development of *C. signifera*, divergences from the observations made on *G. laevis* and *G. victoriana* (GOLLMANN & GOLLMANN, 1991) are stressed.

Stage 20 is very brief in *C. signifera*. The opening of the mouth is soon followed by the appearance of melanophores. A long rectal tube has developed.

During stage 21 (fig. 1D), the cornea becomes transparent, the horseshoe-shaped optic cup becomes faintly visible. Its pigmentation begins in the dorsal part, gradually increasing towards the anterio-ventral side. Late at this stage, blood circulation in the tail fin can be observed. The operculum begins to develop, overgrowing the gill plates, leaving only two broad slits on the ventral side Iridescent chromatophores appear on head, trunk and tail (in *G. laevis* they were first seen at stage 23). They are concentrated in two broad stripes from the eyes to the dorsal edge of the tail myotomes. About half of the embryos have hatched at the end of this stage.

At stage 22 (fig. 2A), only the left slit of the operculum remains. Later on, it develops into the spiraculum. Most embryos have hatched.

At stage 23 (fig. 2B), the horny jaws become visible. Towards the end of this stage, a faint outline of the coiled gut as well as a tiny limb bud can be seen. By now, all animals have hatched.

Labial papillae become discernable only at stage 24 (fig. 2C). A slight reduction of the oral suckers can be noticed.

The inner row of teeth on the upper labium, which appears at stage 25 (fig. 2D), consists of two parts divided by a wide gap The narrow gap in the inner row on the lower labium is hardly visible. The oral suckers have been further reduced to flat, dark-brown rudiments.

At stage 26, brown patches are the only indication of the former position of the oral suckers. The outermost row of labial teeth, which now develops, is about half as long as the other two rows on the lower labium The body wall of the tadpole is highly transparent. No detailed observations of the larvae were made after they had reached stage 26.

DISCUSSION

The embryonic development of *C. signifera* is in many respects similar to that of *Geocrinia* (GOLLMANN & GOLLMANN, 1991). Some of the divergences are probably connected with the different life histories of the two genera (see Introduction). *Crinia signifera* lacks the large yolk reserves necessary for the prolonged terrestrial life of the embryos of *Geocrinia*. The eggs of *C. signifera* are smaller (TYLER, 1989; variation in these

Source : MNHN, Paris

Fig. 1. Selected stages of the embryonic development of *Crinia signifera*. (A) Stage 17, lateral view, 13.4.1989, 18h00. (B) Stage 18, dorsal view, 14.4.1989, 9h45. (C) Stage 19, lateral view, 15.4 1989, 11h40. (D) Stage 21, dorsolateral view, 17.4.1989, 10h50.

Source MNHN, Paris

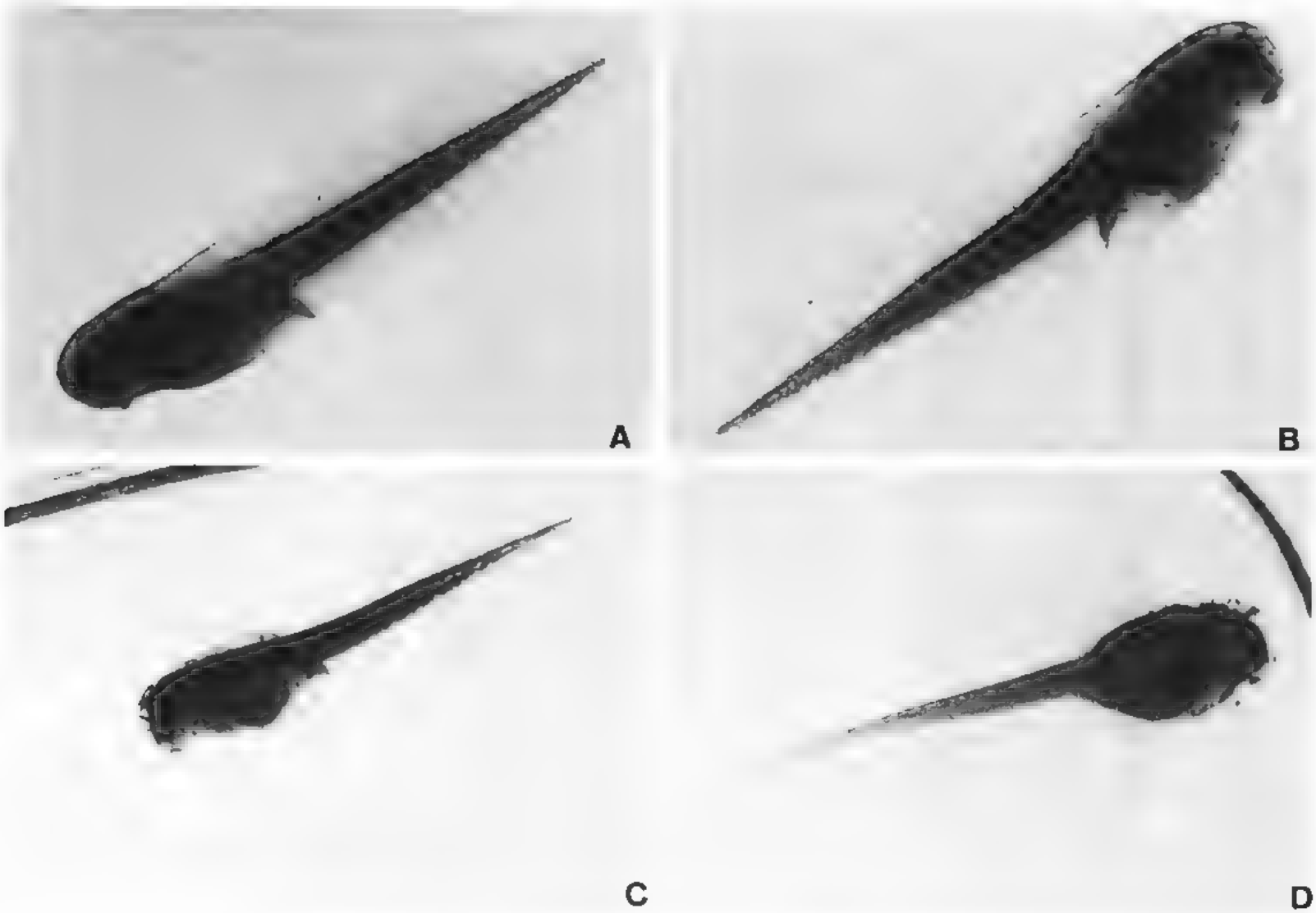

Fig. 2 – Selected stages of the embryonic development of *Crinia signifera*. (A) Stage 22, lateral view, 19.4.1989, 9h10. (B) Stage 23, lateral view, 21.4.1989, 11h00. (C) Stage 24, ventrolateral view, 22.4.1989, 13h00. (D) Stage 25, ventral view, 24.4.1989, 13h15.

Source MNHN, Paris

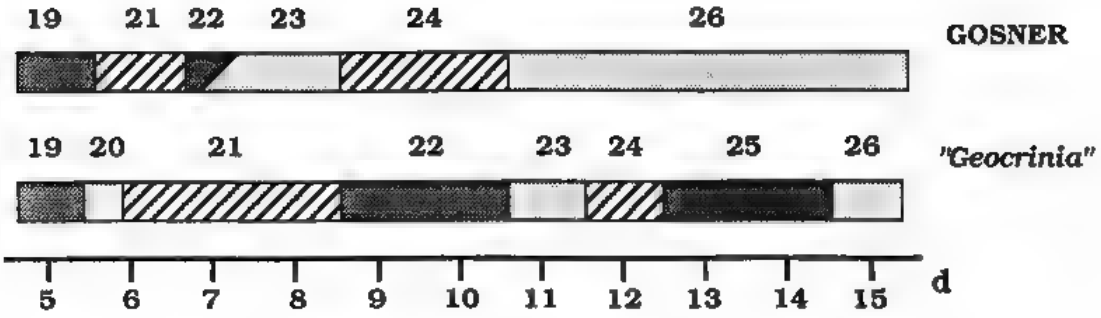

Fig. 3. – Stages in the development of *Crinia signifera*, determined with the staging tables of GOSNER (1960, above) and GOLLMANN & GOLLMANN (1991; below) (d = days since spawning). Because external gills are absent, GOSNER stage 20 could not be identified and GOSNER stages 24 and 25 could not be clearly distinguished.

species is greater than indicated there· WILLIAMSON & BULL, 1989, GOLLMANN & GOLLMANN, 1991) and develop at a faster rate. Under identical laboratory conditions, the development from stage 17 to stage 26 took 16 to 20 days in *Geocrinia* (B. GOLLMANN, unpubl.), but only 12 days in *C. signifera*.

Hatching occurs earlier in *C. signifera* (stage 21 to 23) than in *Geocrinia* (stage 26 or 27). The timing of the resorption of the oral suckers is apparently correlated with the stage at which hatching occurs: maximal development of these organs is usually observed in newly hatched tapdpoles, i.e in earlier stages in North American anurans (GOSNER, 1960) and in later stages in *Geocrinia* (GOLLMANN & GOLLMANN, 1991)

The smaller yolk sacs and the greater transparency of the embryos of *C. signifera* allow the observation of operculum development (which cannot be seen in *Geocrinia*), development of the cornea is also better visible. Therefore it is possible to identify most of the stages of the GOSNER table in embryos of *C. signifera*. A comparison of stages according to the GOSNER table with the staging table used in this study (referred to as " *Geocrinia* table " below) is presented in fig. 3.

The main cause of the great differences between the two tables in the timing of stages is the unusually early and fast development of the operculum, which is probably connected with the absence of external gills. With regard to other features, e.g. the mouth parts, the *Geocrinia* table corresponds well to the GOSNER table. According to GOSNER (1960), oral disc and labial tooth rows begin to differentiate at about stage 23; by stage 26 their essential peculiarities are present. In *Geocrinia* and *C. signifera* labial ridges begin to develop at stage 23; at stage 26 all five rows of oral teeth have formed

Although embryos of *C. signifera* can be staged with the GOSNER table, the use of the *Geocrinia* table seemed preferable: the characters used for stage identification in the latter table were better visible in *C. signifera*, the rapid development of the operculum in *C. signifera* lead to a highly unequal distribution of GOSNER stages over developmental time (fig. 3). Finally, comparative studies of embryology and life history variation can be

Source : MNHN, Paris

conducted in greatest detail among closely related forms. In several myobatrachine genera, e.g. *Geocrinia* (GOLLMANN & GOLLMANN, 1991) and *Pseudophryne* (WOODRUFF, 1972), the GOSNER table cannot be applied during late embryonic development, whereas the *Geocrinia* table provides a useful standard for comparison

RÉSUMÉ

Le développement embryonnaire de la grenouille australienne *Crinia signifera* est décrit et illustré. La plupart des divergences trouvées dans une comparaison avec les grenouilles apparentées du complexe de *Geocrinia laevis* semblent liées à leurs modes de développement différents. L'applicabilité à cette espèce de la table de développement de GOSNER (1960) et de la table modifiée pour *Geocrinia* (GOLLMANN & GOLLMANN, 1991) est évaluée.

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